

Zooplankton Responses to Thin Layers: Integrating Behavior and Physiology

Stephen M. Bollens
Department of Biology, and
Romberg Tiburon Center for Environmental Studies
San Francisco State University
1600 Holloway Avenue
San Francisco, CA 94132
phone: 415-338-3512 fax: 415-435-7121 email: sbollens@sfsu.edu

Award Number: N00014-00-1-0173
<http://userwww.sfsu.edu/~bioocean>

LONG-TERM GOALS

Our long-term goal is to achieve a predictive understanding of the vertical distribution and migration of pelagic animals in the sea by assessing the behavioral and demographic responses of zooplankton and micronekton to their biotic and abiotic environment.

SCIENTIFIC OBJECTIVES

The primary scientific objectives of this project are:

- 1) To determine if zooplankton alter their vertical position and/or migration behavior in response to thin layers.
- 2) To determine the time course of such response (seconds–hours).
- 3) To determine the relevant spatial scales of thin layers to the behavior and physiology of zooplankton.
- 4) To determine how long after erasure of thin layers before the animal returns to a "normal" migration behavior.
- 5) To determine how these responses vary between species and across diverse taxonomic categories (e.g., copepods, larval fish, and microzooplankton).
- 6) How thin layers affect zooplankton feeding (intensity, timing).
- 7) How thin layers affect zooplankton growth and reproduction.

During the last year we have investigated the behavioral and physiological responses of the abundant coastal copepod *Acartia hudsonica* (subgenus *Acartiura*) in the presence of thin layers of the diatom *Skeletonema costatum* (Bochdansky & Bollens, submitted). We also tested the response of a member of the microzooplankton community (the rotifer *Branchionus plicatilis*) to thin layers of *Skeletonema*

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costatum and the flagellate *Nannochloropsis* sp. (Ignoffo 2003, Ignoffo et al., in prep.). Together with previous investigations on herring larvae in response to thin layers (Clay 2003, Clay et al., accepted pending revision) for which we used a similar experimental protocol, we are for the first time able to appreciate the responses of various predator taxa to heterogeneity in prey distributions. While herring larvae and copepods were primarily responding to the salinity distribution in the experimental columns, the distribution of microzooplankton was strongly driven by the distribution of food.

APPROACH

The experimental set-up varies somewhat depending on the organisms of interest. In general, prey organisms (algae, rotifers etc.) are enclosed and concentrated in a layer defined by two density discontinuities using our 2-m tall columnar tank set-up (Fig. 1). Video cameras capture shadow images of zooplankton produced by collimated infrared light that is projected through the tanks. The video images record the position of each individual by panning vertically and parallel to the tanks. The time interval between pans is controlled by a computer program and typically set to one hour. The controls consist of tanks that contain the same number of prey and the same salinity gradients as in the thin-layer treatment, but with an even distribution of prey (homogeneous treatment). Incubations last from 12 h (copepods) to 48 hours (herring). In the experiments with *Acartiura* sp., two physiological variables are added to the analysis: feeding (via fecal pellet production rate) and reproduction (via egg production rates).

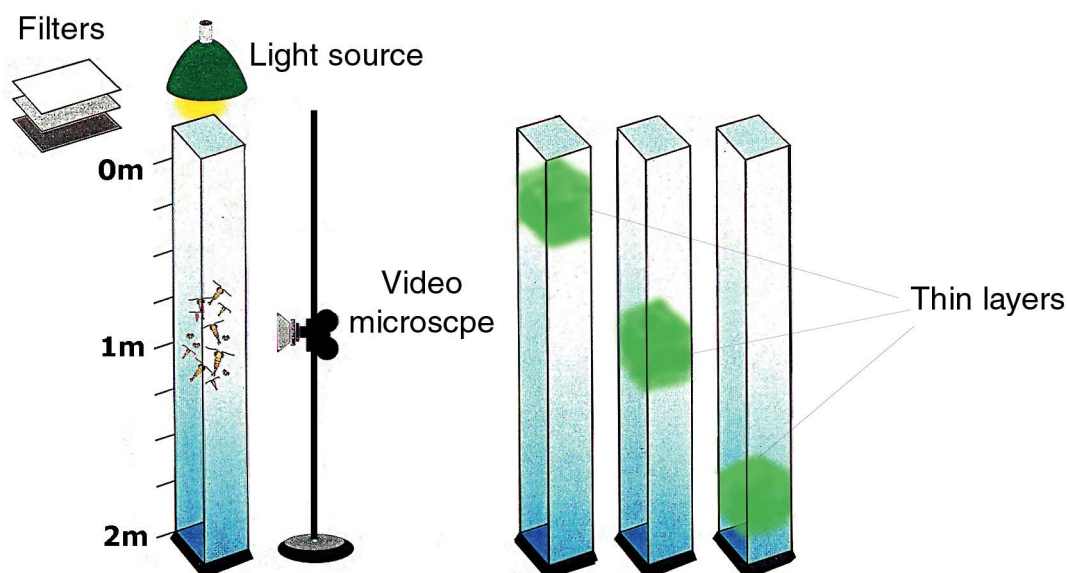


Figure 1. Two-meter high columnar tanks are illuminated by natural light simulators, which incorporate neutral density filters to adjust light intensity. The entire vertical extent of each tank, having one or more thin layers of phytoplankton at various depths, is repeatedly scanned and imaged with an infrared-sensitive video camera to record zooplankton distribution.

WORK COMPLETED

Experiments with herring larvae were completed and a manuscript has been accepted pending revisions at the journal of Experimental Marine Biology and Ecology (Clay et al., accepted). The experimental work on copepods interacting with thin layers was also completed this year and a manuscript is currently in review (Bochdansky & Bollens, submitted). We have finished a series of experiments using rotifers as predators and diatoms and nanoflagellates as food. The analysis of these data is almost completed and a manuscript is in preparation (Ignoffo et al., in preparation).

RESULTS

Brachionus plicatilis. The aggregation of predator in response of the aggregation of prey was long-lived (i.e. many hours) and lasted until the food was depleted (Ignoffo et al. 2003). Rotifers preferred thin layers of *Nannochloropsis* sp. over thin layers of the diatom *Skeletonema costatum*. When given a choice, they accumulated more rapidly and more strongly in the flagellate thin layer than in the diatom thin layer, whereas there was only a subtle aggregation due to the salinity gradients in the tanks. In some cases, rotifers avoided the location of highest prey abundance and formed two peaks at the edge of the prey patch (Fig. 2a).

Clupea harengus. The distribution of herring larvae in the tanks was significantly affected by the haloclines and the distribution of rotifers. During the 48 hours time series rotifers aggregated at the surface, the bottom and in the haloclines which in turn was reflected by increased herring distribution at these sites (Fig. 2b).

Acartia hudsonica. In a series of experiments, the same quantity of a diatom culture (*Skeletonema costatum*) was presented in two distinct distributions: 1) The diatoms were homogeneously distributed a concentration of $25 \mu\text{g C L}^{-1}$ throughout the water column. 2) The diatoms were mixed into a volume corresponding to 1/8 of the entire water column in the center of the tank and at 8 times higher concentration ($200 \mu\text{g C L}^{-1}$). These concentrations were chosen according to the numerical response of egg production to food availability (data not shown). Two hundred $\mu\text{g C L}^{-1}$ represents a food environment that leads to a maximum egg production, compared to $25 \mu\text{g C L}^{-1}$ at which egg production is severely food limited. Additional experiments revealed that egg production reflects feeding conditions with a delay of 12-24 hours (data not shown).

We found that the copepod *Acartia hudsonica* consistently aggregated in thin layers, which was likely the result of slower swimming speeds at higher feeding intensity. However, this effect was short-lived. Over longer time scales (i.e. 12h), the copepods on average did not more densely aggregate in the presence of aggregated food than in homogeneous treatments using three different indices of aggregation. One example is shown in Fig. 2c. Feeding (measured via fecal pellet production) was significantly influenced by the distribution of prey in the tanks with more fecal pellets produced in the homogeneous environment but the difference between treatments was small. Reproductive rates (measured using egg production as a proxy) were not significantly influenced by the spatial distribution of food (i.e. homogeneous vs thin-layer treatments). In choice experiments (data not shown), *Acartia* was able to find and actively swim into patches of diatoms when they were only centimeters away from the food source. Perception over longer distances did not seem to occur. Our results suggested that *Acartia* could take advantage of thin-layers during short and intermittent encounters with patches of prey despite the short duration individuals stayed in the food patches.

However, diurnal migration behavior and the salinity gradients more strongly influenced the distribution of copepods in the tanks than food. These behavioral and physiological responses contrasted strikingly to the behavior of the rotifer *Branchionus plicatilis*.

Our results which separate physical from biological effects are very important for the interpretation of observations in which strong density gradients are frequently correlated with the abundance of prey organisms (e.g., Harder 1968, Lougee et al., 2002). These results provide additional, corroborating evidence in support of earlier studies (e.g., Bollens and Frost 1989, 1991, Bollens et al. 1992, 1993, 1994) that individual zooplankton can and do exercise flexible, plastic migration behavior in responding to their biotic and abiotic environment. Our most recent experiments underscore that thin layers have very different effects depending on the predator under investigation. The order of panels in Fig. 2 reflects this differential behavior of three types of zooplankton to thin layers of prey, from most responsive (microzooplankton) at the top to least responsive (copepods) on the bottom (Fig. 2).

IMPACT/APPLICATION

Our results are consistent with our earlier findings (Lougee et al. 2002) and suggest that for both herring larvae and copepods, physical factors are a stronger cue for their distribution than the distribution of prey organisms. The published literature abounds with speculations on how prey patches affect aggregation of micronekton and mesozooplankton (e.g. Sameoto 1984, Daro 1988) and numerous models are based on algorithms that suggest that retention in patches of high food concentrations are due to behavioral changes and changes in swimming speeds (Tiselius et. al 1993, Leising & Franks 2000, Leising 2001). However, many of these assumptions are based on experiments performed in containers approximately one order of magnitude smaller than the tower tanks in our study (e.g. Saiz et al. 1993). It is therefore possible that the studied organisms were not able to express their full behavioral repertoire (including vertical migration in the water column) under these circumstances. Seen from the point of view of the individual organism, physical parameters may be more reliable indicators for the location of prey than ephemeral patches of prey without underlying physical features. An important result of our experiments with copepods is that despite strong differences in the distribution of prey, behavioral adjustments and physiological processes in individuals may dampen the effect of environmental variability considerably.

These findings represent an important contribution to the Thin Layers program as they revise our understanding of the response of various zooplankton taxa to thin layers of prey. This research is relevant to Navy interests because zooplankton and micronekton dominate the scattering of sound in the water column at frequencies between 10 kHz and 10 MHz; the Navy must therefore be able to predict where and when sound scattering layers will occur. Moreover, this research is broadly relevant to oceanic biology, for depth selection is important not only in population biology and community ecology of zooplankton, but also in understanding the vertical flux of materials, nutrients and energy from surface waters to depth in the ocean and from thin layers into the ambient water.

RELATED PROJECTS

This research is relevant to virtually all of the many field studies previously and currently being undertaken within the “Thin Layers” program.

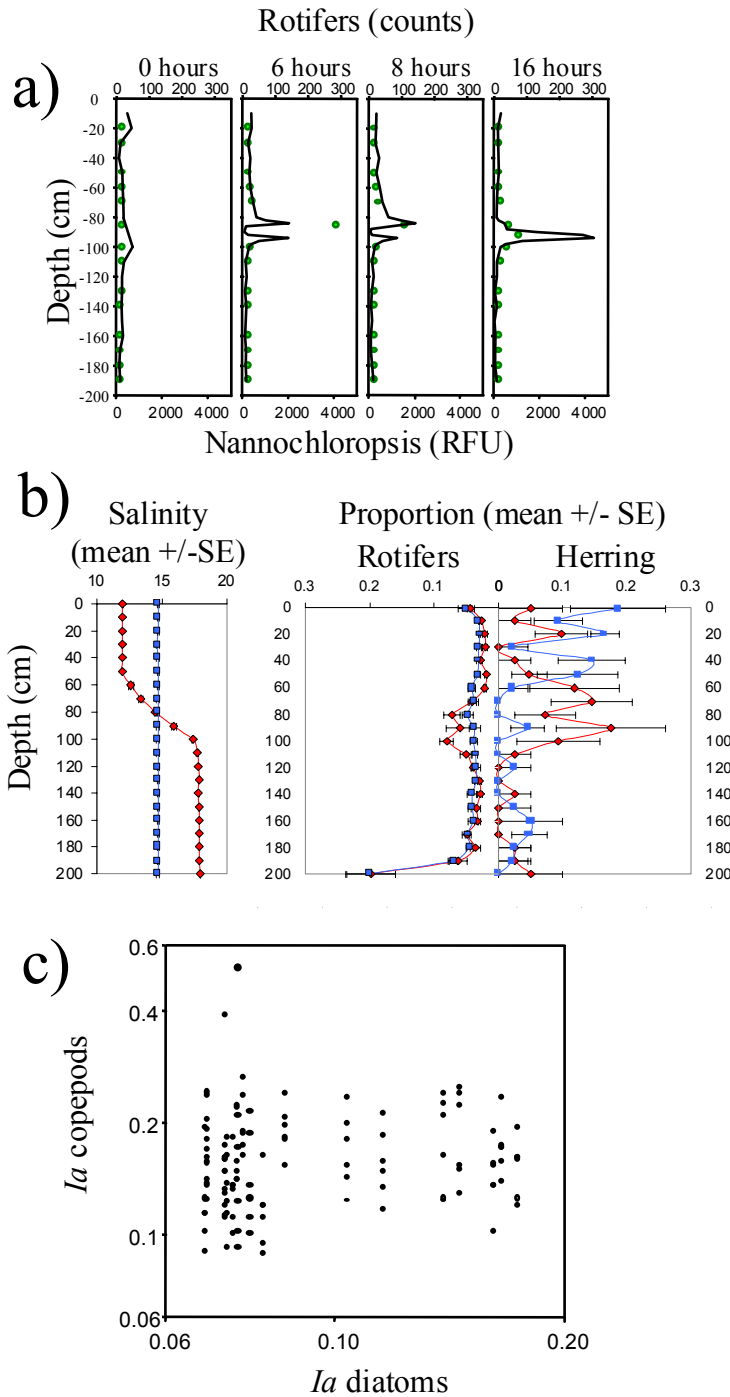


Figure 2. a) Time series of a distribution of rotifers (*Brachionus plicatilis*, solid lines) in response to a thin layer of *Nannochloropsis* sp. (circles). After 6 h double peaks of rotifers formed around the fluorescence peak. The rotifers fed on the prey cells until a prominent peak of rotifers was left in the center of the tank (from Ignoffo et al., in prep.). b) Representative example of the distribution of 5-d old herring larvae in response to a rotifer thin layer. Diamonds = stratified (thin layer treatment), squares = homogeneous treatment (from Clay et al., accepted). c) Index of aggregation (Ia) of *Acartia hudsonica* in response to Ia of the diatom *Skeletonema costatum* in various treatments. Although the copepods showed an initial (2–4 hrs) positive response to thin layers, overall, they did not aggregate more strongly in response to thin layers (open symbols) compared to a homogeneous distribution of diatoms (closed symbols) (from Bochsansky & Bollens, submitted).

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